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ORIGINAL ARTICLE

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Reduced nest defence intensity and improved breeding success in terns as responses to removal of non-native American mink

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Abstract Lack of parental experience or differences in reproductive effort may lead to variation in nest defence behaviour among individuals in a prey population. In this experimental study, we analysed nest defence behaviour using a model of an American mink, *Mustela vison*, a non-native predator, at colonies of arctic terns, *Sterna paradisaea*, in two large areas where mink had been removed and two comparable control areas with mink in the south-western archipelago of Finland, Baltic Sea, in June 2000. Furthermore, we recorded breeding success of arctic terns in the same four areas during 1998–2001. Arctic terns took higher risks in nest defence in control areas and in a short-term (mink-free for 2 years) removal area than in the long-term (mink-free for 8 years) removal area. Thus, colonies with recent experience of mink were more active in defending their offspring. The breeding success of arctic terns was significantly higher in mink-removal areas than in control areas. We conclude that arctic terns modify their nest defence behaviour in the presence of mink. However, they cannot defend their nests sufficiently against this mainly nocturnal predator, since their breeding success is reduced in areas where mink are present.

Keywords Baltic Sea · *Mustela vison* · Parental care · Predator removal · Reproductive success

Introduction

Parental care includes the difficulty in balancing between current and future reproduction (Clutton-Brock 1991). Nest defence is a costly form of parental care in which parents have to weigh the risks (e.g. death or injury) of defending the nest and offspring against the benefits (increased survival of the offspring). Parents should invest more in large than in small broods, because the benefits of defending the brood increase with offspring number (parental investment theory; Trivers 1972; see also Redondo 1989). Therefore, the optimal result of parental care is achieved when parents are able to maximise their own fitness (Williams 1966; Montgomerie and Weatherhead 1988). In colonial birds, colony size may affect nest defence intensity: in larger colonies the total sum of nest defence is higher but the individual investment is lower (Allainé 1991; Arroyo et al. 2001).

Nest defence intensity is furthermore affected by factors such as quality of offspring, offspring age, type of predator and parental experience (Montgomerie and Weatherhead 1988; Redondo 1989; Clutton-Brock 1991; Hakkarainen and Korpimäki 1994; Tolonen and Korpimäki 1995; Dale et al. 1996). Nest defence behaviour on the individual level has been suggested to be influenced by either constraint or restraint mechanisms (Williams 1966; Curio 1983). According to the constraint hypothesis, the intensity of nest defence should be affected by parental experience. For experienced parents, the probability that chicks will survive and reproduce also increases for reasons other than those related to nest defence. Therefore, for more experienced parents offspring will be more valuable, and they should also increase investment in the form of nest defence. Furthermore, experience in confronting a nest predator should result in changes in nest defence as such at both individual and population levels (Lemmetyinen 1972; Montgomerie and Weatherhead 1988). Parents may therefore learn how to confront the predator without exposing themselves to high risks of predation and may thereby optimise their nest defence behaviour against their own risk-taking. According to the restraint hypothesis, nest defence is not related to parental experience but to the fact that breeding individuals may balance their nest defence in relation to current risks and future

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reproduction. Separating between the constraint and restraint hypotheses in field studies may be difficult, but most studies support the constraint hypothesis (e.g. Desrochers 1992; Wiebe and Martin 1998; Laaksonen et al. 2002; but see Lambrechts et al. 2000).

Breeding success of birds is affected by many factors, e.g. weather conditions, food availability and natural enemies (Newton 1998). In particular, non-native predators may cause severe decreases in breeding success of seabirds breeding on islands (Kilpi 1995; Seto and Conant 1996; Craik 2000a), which normally act as refuges from native ground-living predators. It has been proposed that the native fauna is naïve towards introduced and re-introduced predators because they lack behavioural traits (constraints) or evolutionary adaptations (restraints) to manage the intruders (Banks 1998; Berger et al. 2001; Short et al. 2002). Therefore, besides impacts on breeding success, we also need to know more about the behavioural responses of prey populations to introduced predators.

In Europe, the non-native American mink, *Mustela vison* (hereafter "mink"), has turned out to be an important predator of sea- (Andersson 1992; Craik 1997; Nordström et al. 2002, 2003) and wetland birds (Ferreras and Macdonald 1999) and of small mammals (Woodroffe et al. 1990; Aars et al. 2001; Banks et al. 2004), as well as being a superior competitor against smaller mustelid species (Sidorovich et al. 1999). Clode et al. (2000) studied the nest defence behaviour of terns and gulls on the western coast of Scotland and found that the defence intensity of terns was higher on islands inhabited by mink than on islands that had not yet been colonised by mink.

In this study, we tested the intensity of nest defence behaviour in colonial arctic terns, *Sterna paradisaea*, by conducting trials with a model mink at colonies in areas where mink were abundant and in areas where mink had been experimentally removed. We wanted to find out how parental experience of the nest-depredating mink affects intensity of nest defence. We predicted that in control areas with more experience of mink, nest defence intensity would be higher than in removal areas with less experience of mink. Because we have one long-term and one short-term removal area (mink-free for 8 and 2 years, respectively), we were also able to examine the effect of time since removal. Finally, we present results of breeding success for colonial arctic terns in these four areas and discuss the effects of behaviour on reproductive traits.

Methods

Study areas

The study was conducted in the Archipelago National Park (59°55′ N, 21°50′ E) in the central part of the Baltic Sea, in south-western Finland. In a 72-km^2 area in Nauvo, Trunsö (hereafter called R1), mink had been removed since autumn 1992, and in a 125-km^2 area in Korppoo, Utö-Jurmo (R2), mink had been removed since autumn 1998. The R1 area has been nearly mink-free since spring 1993 and the R2 area since spring 1999 (see Nordström et al. 2002, 2003 for details of mink removal). Two comparable control areas were established: one area in Dragsfjärd, Vänö (100 km^2, C1) in 1994 (enlarged in 1998) and one area in Korppoo, Brunskär (130 km^2, C2) in 1998. The areas consist of small (mainly <2 ha), treeless islands with sparse vegetation (see Nordström et al. 2002, 2003 for location and habitat composition of the four areas).

Study species

Mink have established self-maintaining populations in Finland since the 1950s and since the late 1970s have been widespread and abundant in the south-western archipelago (Kauhala 1996). This species is a generalist, mainly nocturnal, predator that primarily subsists on birds, small mammals, fish and amphibians (Dunstone and Birks 1987; Niemimaa and Pokki 1990). In the Baltic Sea and the British Isles, the mink have had local devastating effects on several colonial seabirds such as the arctic tern; the common gull, *Larus canus*; the black-headed gull, *Larus ridibundus*; the razorbill, *Alca torda*; and the black guillemot, *Cepphus grylle* (Andersson 1992; Kilpi 1995; Craik 1997, 2000a; Clode and Macdonald 2002; Nordström et al. 2002, 2003).

The arctic tern is one of the most typical and common seabirds in the northern Baltic Sea (von Numers 1995). In our study areas it usually breeds in small (10–40 pairs) colonies, although colonies up to 100 pairs as well as single breeding pairs may occur. Long-lived seabirds usually show high colony and nest site fidelity, but breeding sites may be abandoned after heavy predation (Burger 1982; Kilpi 1995; Whittam and Leonard 1999). Predation by mink in an arctic tern colony is most often targeted on nestlings, while eggs and adults are predated less frequently (M. Nordström, personal observation). Mink are furthermore known for their high levels of killing above the amounts they can eat (e.g. Hario 2002).

Nest defence trials

To examine differences in nest defence behaviour of arctic terns among the R1, R2, C1 and C2 areas, a stuffed model of a mink specimen was placed in 24 tern colonies in June 2000. The covered mink model was placed and revealed in the middle of the tern colony, within 1 m of the nearest nest. When the covered model was placed in the colony, terns usually alarm-called at a distance of >5 m from the observer but did not perform any real attacks. After the cover was removed, the observer immediately moved to 40–50 m away on the same island, and from here the behaviour of terns was recorded by two observers without the use of a hide. Terns detected the model within less than 1 min and started to flock above it. After they had detected the model, they appeared to ignore the observers (M. Nordström made the observations, M. Ahola recorded). After the first dive by a tern towards the model, the trial started and lasted for 15 min. Only one trial was made in each colony. We performed time sampling (Martin and Bateson 1986) by counting the number of dives per minute within 1 m of the model (estimated on basis of its length) and the number of birds flocking within 3 m above it. We noted dives and number of flocking birds each minute of the trial because there might be a notable variation in these variables during the experiment. In particular, the number of birds may be highest in the beginning of an experiment and decrease towards the end (Lemmetyinen 1971). In addition, we counted the total number of arctic terns in the colony. Nine of the colonies were in the R1 area where mink had been removed for eight breeding seasons, six colonies were in the R2 area with mink removed for two breeding seasons, and four and five colonies were in control areas C1 and C2, respectively, i.e. in areas where mink have been occurring since the late 1970s. In the long-term removal area, R1, tern colonies had existed on the studied islands for a considerable time: three colonies since at least 1993, two since 1994, two since 1995, one since 1996, and one since 1999. In the short-term removal area, R2, all colonies had existed since at least 1998. In control areas, colonies had existed in C1 at least since 1994 and in C2 at least since 1998. Colony size

Table 1 Number of arctic tern colonies where breeding success was recorded (left of the slash) and number of colonies where total breeding failure occurred (right of the slash) in 1998–2001 in each study area (*R* removal areas, *C* control areas). Mink removal started in autumn 1992 in R1 and in autumn 1998 in R2

Area	1998	1999	2000	2001
R1	-	6/1	16/1	12/3
R2	6/2	13/1	13/4	8/1
C1	5/4	7/2	6/3	4/2
C2	13/12	15/4	8/4	10/6

ranged from 10 to 35 pairs, all with chicks or eggs, and they all contained arctic terns; in two colonies (one in R1 and one in C2) 40% and 29% of the terns were common terns (*Sterna hirundo*). Arctic and common terns were not distinguished in the nest defence trial, and these two colonies had 20 and 25 pairs of arctic terns. However, these two species act in a similar way when exposed to a model of a predator (Lemmetyinen 1971). The distance between colonies within an area was on average 3.0 km (±0.35 SE), while the distance between two neighbouring areas was ca. 10–15 km and between the two most distant areas, C1 and C2, was 40 km. Therefore, it is unlikely that the same tern individuals were visiting different colonies within or between areas during 18–29 June 2000, when these nest defence trials were conducted. In that period, chicks of terns were on average 2–3 weeks old. All the islands with tern colonies are unoccupied by humans, and most of the studied islands belong to the Archipelago National Park, where landing by the public is prohibited during the breeding season of birds. Therefore, behavioural changes induced by earlier experience of humans are unlikely sources of bias.

Breeding success

Breeding success of arctic terns was studied in four breeding seasons (1998–2001), except for R1, where data for arctic terns are missing for 1998. Numbers of studied arctic tern colonies can be found in Table 1. Nests were counted in early June in all four study areas, and breeding success was checked in late June and early July. We made a simple estimate of breeding success in which the total number of fledged young and large chicks (>14 days old) was divided by the total number of breeding pairs (based on nest counts) (Walsh et al. 1995). Some nests, with eggs and small chicks, of late-breeding pairs were not included in the analyses. Late breeders commonly fail to breed, and therefore our estimate of breeding success may be consistently overestimated (Nisbet and Welton 1984; Kilpi 1995; Craik 2000b). However, this method may give a slight underestimate of breeding success as well, since some smaller chicks not included may survive to fledging, but it is comparable when assessing the productivity in different areas and colonies. Because of the large areas and the large number of colonies, we could make only one visit each year to count fledglings. We also calculated the body condition index for arctic tern chicks in 2000 by dividing body mass by wing length. This was done approximately 1 week prior to fledging, and only chicks with primary feathers growing were included. Mass was measured to the nearest 1 g with a Pesola 300-g spring balance, and wing length was measured to the nearest 1 mm with a ruler using the maximum method (Svensson 1992).

Data analyses

Data from the trials with the mink model were analysed using repeated measurements ANOVAs in the procedure MIXED (SAS statistical software 8.01), which uses the maximum likelihood estimation (Littell et al. 1996). The number of dives within 1 m and the number of birds flocking within 3 m above the model were the dependent variables, while treatment (TRT, removal or control), area nested within treatment [AREA(TRT)], two removal and two control areas), the time of the trial (TIME; 1–15 min), and the number of individuals in the colony (COLONY SIZE) were independent variables. Colony nested within area and treatment was the subject in the analyses, and time was the repeated factor. Trials were conducted during daylight, between 8 a.m. and 8 p.m., but the moment at which the trial was conducted did not have an effect on the nest defence behaviour [ANOVA $F_{1,358}^{(\text{DIVES})} = 2.75$, $P=0.10$; ANOVA $F_{1,358}^{(\text{FLOCKING})} = 0.13$, $P=0.72$]. We started with a full model and removed all non-significant interactions. To meet the assumptions of normality, the data was $\log_e$ transformed. Figures 1 and 2 show back-transformed results with least-square means.

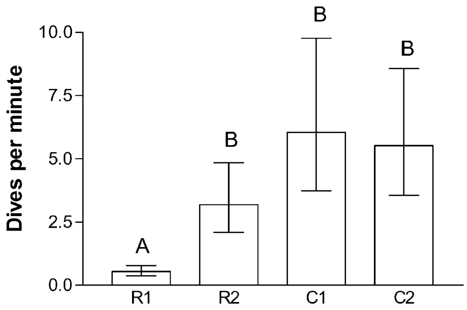

Fig. 1 Dives per minute by arctic terns within 1 m (least-square means ± SE) at the mink model in two removal (*R1*, *R2*) and two control (*C1*, *C2*) areas. Different letters above the bars indicate significant differences between areas, and the same letter indicates no significant difference (a posteriori Tukey test)

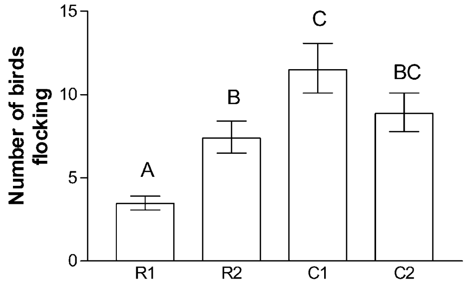

Fig. 2 Number of arctic terns flocking per minute (least-square means ± SE) above the mink model in two removal (*R1*, *R2*) and two control (*C1*, *C2*) areas. Different letters above the bars indicate significant differences between areas, and the same letter indicates no significant difference (a posteriori Tukey test)

Differences in breeding success were analysed using a generalised linear model with breeding success (number of fledglings/total number of pairs) as the dependent variable and the independent variables treatment, area(treatment), year (1998–2001, class variable), and colony size (continuous variable). We used the procedure GENMOD in SAS statistical package 8.01 with Poisson distribution for these analyses.

To analyse colonies with total breeding failure (no fledglings) with mink removal, we used a logistic regression in procedure GENMOD with binomial distribution and logit link function. The dependent variable was breeding result (total breeding failure or ≥ 1 fledgling in a colony), and the independent variables were treatment, area(treatment), year (1998–2001, class variable), and colony size (continuous variable). In analyses of breeding success and total breeding failure, the initial level was used as baseline covariate, but since they were non-significant ($P>0.6$), the covariates were removed from the final analyses. To test body condition index of chicks, we used an ANOVA in procedure MIXED, with a posteriori Tukey-tests to make paired comparisons of treatment and areas. The date was included in the model to control for growth of chicks.

Results

Nest defence

In the R1 area terns showed the lowest nest defence intensity in terms of attacks within 1 m of the mink model, while the response by terns in the R2 area and in the two control areas was higher (Fig. 1, Table 2). The effects of the number of birds in the colony and time of trial (1–15 min from the beginning) were not significant. There were also fewer birds flocking within 3 m above the model in the R1 area than in the other three areas (Fig. 2, Table 3). The flocking number in R1 differed significantly from the other three areas, and the number in R2 differed from C1 but not from C2 (Fig. 2). For the number of birds flocking, the effect of trial time was also important; there were more birds flocking above the model at the beginning than at the end of the 15-min trial period. The treatment by time interaction was not significant, so it was removed from the analyses. Colony size affected the number of individuals flocking above the model but not the intensity of dives (Tables 2, 3). According to the a posteriori tests, in R2 dive rates and flocking numbers did not differ significantly from those in control areas, although both appeared to be lower (Figs. 1, 2).

Breeding success

Arctic terns bred more successfully in mink-removal than in control areas (Fig. 3, Table 4). There was also a significant year effect, with the year 1999 showing the highest mean number of fledglings produced per pair. Since there were no significant year by treatment interactions, the term was removed from the final analyses. Total breeding failures were more common in control areas than in removal areas: on average 50% of the colonies in C1 and 57% of the colonies in C2 failed to raise any fledglings, while the corresponding proportion was 15% in R1 and 18% in R2 (1999–2001). Before the initiation of mink removal, in 1998, this proportion in R2 was 33% (Tables 1, 4).

In control areas signs of mink, such as fresh scats, tracks, caught prey and sightings, were detected on 60% of islands containing tern colonies over the course of the study. On the other hand, mink presence is not always detectable because they may not leave any visible signs and prey items may be hidden and difficult to find. In the R1 area 1 tern colony of 6, with 10 nests, was visited by a mink in 1999, leading to total breeding failure. Similarly, in the R2 area, mink visited 3 of the 13 colonies in 2000, and these colonies showed the following breeding successes: 0.4, 0.21, and 0.05 fledglings/pair. Colony size did not affect the breeding success, but smaller colonies were more likely to experience total breeding failure than were large colonies (Table 4). Mink removal did not have any obvious effect on the body condition index of arctic tern chicks in summer 2000 (Table 5; ANOVA: $F_{1,135}$=2.54, P=0.11). The age of chicks, measured by wing length, with measurement date as the covariate, was comparable in all areas (Table 5; ANOVA $F_{3,133}$=2.20, P=0.09).

Table 2 Repeated measurements ANOVA table testing the effects of treatment (*Trt*), area [*Area(Trt)*], trial time, and colony size on the number of dives within 1 m of the mink model

Source	NDF	DDF	*F*	*P*
Trt	1	20	16.95	0.0005
Area(Trt)	2	20	7.63	0.034
Time	14	20	0.73	0.7194
Colony size	1	20	0.27	0.6119

Table 3 Repeated measurements ANOVA table testing the effects of treatment (*Trt*), area [*Area(Trt)*], trial time, and colony size on the number of individuals flocking above the mink model

Source	NDF	DDF	*F*	*P*
Trt	1	20	194.12	<0.0001
Area(Trt)	2	20	74.97	<0.0001
Time	14	20	5.22	0.0005
Colony size	1	20	75.93	<0.0001

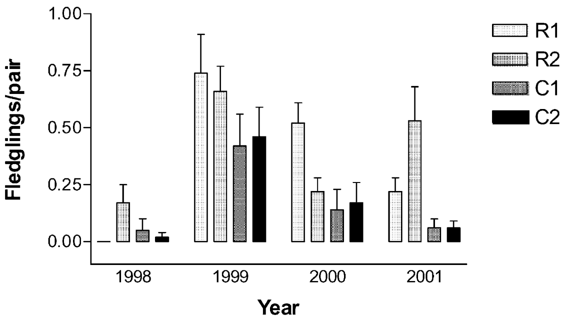

Fig. 3 Breeding success (mean number of fledglings produced per pair ± SE) of arctic terns in removal (*R1*, *R2*) and control (*C1*, *C2*) areas during 1998–2001. Data are missing for R1 in 1998. Mink removal started in autumn 1998 in the R2 area

Table 4 Effects of treatment, area(nested within treatment), year, and colony size on the breeding success and total breeding failure in colonies of arctic terns

Source	*df*	Success χ^2	*P*	Failure χ^2	*P*
Treatment	1	4.87	0.027	11.71	0.0006
Area(Trt)	2	0.17	0.92	0.17	0.92
Year	3	13.73	0.003	18.81	0.0003
Colony size	1	0.14	0.70	10.76	0.001

Table 5 Number of individuals (*n*), number of colonies of chicks (*nc*), body condition index (*bc index*), average wing length, and body mass (±SE) for arctic tern chicks in two removal (*R1* and *R2*) and two control (*C1* and *C2*) areas. Different letters indicate significant differences between areas, and the same letter indicates no significant difference (after a posteriori Tukey test). The date when chicks were measured was included as the covariate when analysing the data

Area	*n*	nc	bc Index	Wing (mm)	Mass (g)
R1	58	8	0.81^{A} (±0.02)	122.3^{A} (±4.3)	96.0^{AB} (±2.3)
R2	37	7	0.84^{B} (±0.02)	134.6^{A} (±4.3)	110.2^{A} (±2.0)
C1	22	6	0.79^{AB} (±0.03)	135.0^{A} (±7.1)	103.1^{B} (±3.9)
C2	21	6	0.90^{AB} (±0.03)	115.1^{A} (±4.9)	101.3^{AB} (±3.0)

Discussion

The removal of mink led to the following main responses. First, nest defence intensity (as estimated by the number of dives and birds flocking above the mink model) of arctic terns was significantly lower in the area that had been mink-free for eight breeding seasons than in both the short-term (mink-free for two breeding seasons) mink-removal area and the two control areas with permanent presence of mink. Second, the breeding success of arctic terns was higher in both mink-removal areas than in the control areas. Furthermore, more total breeding failures occurred in areas with mink than in removal areas.

On the basis of our results we cannot distinguish whether the parental behaviour is due to constraint or restraint mechanisms. Arctic terns may have learnt to consider mink as a threat for both adults and young and may have altered their nest defence behaviour through experience (constraint). In the R1 area arctic terns took lower risks in brood defence against the mink model than in the control areas, suggesting that terns breeding on mink-removal islands did not consider mink as serious a threat as did terns in the control areas with mink. A further indication of this is that the tern colonies showing the least risky behaviour were in the R1 area, which had been mink-free for 8 years. Terns in the R2 area, which had been mink-free for only 2 years, showed intensity of nest defence similar to that of the colonies in the control areas. Prey populations with no earlier experience of a predator may respond little, or not at all, because they may not consider the predator as a threat (Lemmetyinen 1972; Clode et al. 2000). Our results indicate that nest defence behaviour may change even within a rather short time period, even though the arctic tern is a long-lived species (up to >30 years) (Cramp 1985). In the control areas, the birds probably have fresh experience of mink, and therefore their nest defence behaviour is more intense. Arctic terns in the removal areas may still consider mink as a threat, but their nest defence behaviour has decreased with the decrease in predation (Lima and Dill 1990; Veen et al. 2000). On the other hand, terns in the long-term removal area may be taking restrained risks in nest defence because they have decided not to defend their nestlings intensely, since the loss of nestlings in one year has little effect on their lifetime reproductive success, whereas in control areas with permanent mink, birds may choose to take higher risks, since predation risk is high in every year. In Scotland, arctic terns showed a lower response to a mink model in mink-free areas than in areas that mink had not yet reached. This suggests that the higher aggression against the model in mink-inhabited islands was altered by experience of mink (Clode et al. 2000). However, in addition to the results of Clode et al. (2000), this study, in which predation pressure was experimentally reduced, amplifies those findings by showing that nest defence behaviour of birds accustomed to mink may be decreased once mink predation pressure diminishes.

Arctic tern colonies experienced more total breeding failures and lower numbers of offspring per nest in control areas than in removal areas. Mink may reduce the breeding success of arctic terns both directly and indirectly, by killing chicks and causing nestling starvation by deterring adults from attending to their young (Nisbet and Welton 1984; Burness and Morris 1993). The latter is apparently a result of repeated “upflights” and even colony abandonment at night, since seabirds cannot defend against a nocturnal predator (Hunter and Morris 1976).

A significant among-year variation in breeding success was also found for arctic terns. For seabirds, extrinsic factors, such as weather in a given year, may affect the breeding success at a higher level than predation (Owen and Norderhaug 1977; Beck and Finck 1985; Bunin and Boates 1994) because eggs and chicks of terns may have better survival in years with favourable weather conditions. During this study, more-than-average amounts of rain fell in the breeding season of 1998 (Banks et al. 2004), and it is likely that this may have reduced the breeding success.

To conclude, this study has shown that non-native mink reduce the breeding success of arctic terns which recognise them as a predator and can vary their nest defence behaviour to meet the level of predation risk. Therefore, improved offspring survival is probably one of the main reasons for increases in breeding densities of arctic terns in our mink-removal areas (Nordström et al. 2003). Measurements of nest defence intensity and breeding success together indicate that terns in the area with the highest number of offspring per pair showed the lowest nest defence intensity. This is the opposite of what is predicted by the parental investment theory (Trivers 1972; Montgomerie and Weatherhead 1988; Redondo 1989). These results therefore suggest that the experience of predation may be a stronger influence than offspring number on nest defence intensity of arctic terns.

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